Complex battlefields favor strong soldiers over large armies in social animal warfare

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In social animals, success can depend on the outcome of group battles. Theoretical models of warfare predict that group fighting ability is proportional to two key factors: the strength of each soldier in the group and group size. The relative importance of these factors is predicted to vary across environments [F. W. Lanchester, *Aircraft in Warfare, the Dawn of the Fourth Arm* (1916)]. Here, we provide an empirical validation of the theoretical prediction that open environments should favor superior numbers, whereas complex environments should favor stronger soldiers [R. N. Franks, L. W. Partridge, *Anim. Behav.* 45, 197–199 (1993)]. We first demonstrate this pattern using simulated battles between relatively strong and weak soldiers in a computer-driven algorithm. We then validate this result in real animals using an ant model system: In battles in which the number of strong native meat ant *Iridomyrmex purpureus* workers is constant while the number of weak non-native invasive Argentine ant *Linepithema humile* workers increases across treatments, fatalities of *I. purpureus* are lower in complex than in simple arenas. Our results provide controlled experimental evidence that investing in stronger soldiers is more effective in complex environments. This is a significant advance in the empirical study of nonhuman warfare and is important for understanding the competitive balance among native and non-native invasive ant species.

warfare | Lanchester's laws | habitat complexity | invasive ants | social insects

Significance

Warfare is fundamental to the outcome of competition in social species from humans to insects and is of global interest and appeal to scientific and public audiences alike. Although theory predicts that the environment in which group battles take place will affect the optimal strategy, empirical tests are difficult. Here, we use simulated battles in a gaming construct to demonstrate that investing in smaller armies of stronger soldiers is more effective in complex battlefields. We then use a real-world system for group battle studies—social ants—to validate our findings in an empirical setting and find that small armies of large ants perform better against large armies of small ants in complex environments.

Our understanding of the mechanics of group combat in social animals is informed by Lanchester's laws, which were originally developed to describe technological advances in warfare occurring in the period before the First World War, particularly the advent of military aircraft (1). These laws state that the outcome of group battles depends on the individual fighting strength of soldiers or units and the number of units in opposing armies (1) and were later generalized according to the following rule (2–5):

$$\frac{m_0^\theta - m_t^\theta}{n_0^\theta - n_t^\theta} = \frac{\alpha_n}{\alpha_m}, \qquad [1]$$

where α_n and α_m are the individual fighting strengths of units in opposing armies n and m, n_0 and m_0 are the number of units in each army at the beginning of combat, n_t and m_t are the number of units in each army at any given time t, and θ describes the relationship between group fighting ability and group size. The modern adaptation of Lanchester's laws to nonhuman combat (2–4) states that at any time in a battle, Eq. **1** will be satisfied. Note that here, we use the terms "soldiers" and "units" interchangeably to refer to individuals within armies or groups.

The relative importance of individual fighting strength and army size, defined by the value of θ, varies. Numerical superiority is relatively less important when battles resemble a series of one-on-one duels (Lanchester's Linear Law, $\theta = 1$) and more important when armies can focus attacks and outnumber each soldier of the opposing force in every contest (Lanchester's Square Law, $\theta = 2$) (1–5). Lanchester's original formulation was based partly on the prediction that advances in weapons technology would make it easier to concentrate attacks and would therefore push the balance toward the Square Law (1). These laws were first applied to nonhuman warfare by Franks and Partridge (2, 3), and the most productive real-world model systems for experimental tests of nonhuman group combat have been social insects such as ants since they regularly engage in large battles with high mortality (5–7). Group size significantly affected group fighting ability in the red imported fire ant *Solenopsis invicta* (Buren 1972), but the relationship was closer to Lanchester's Linear Law than to Lanchester's Square Law (estimated $\theta = 1.04$) (8). In red wood ants *Formica rufa* (Linnaeus, 1761), although both enemy group size and individual size of enemy workers were positively associated with group attrition rate, individual strength and fighting behavior were found to be as important or more important than enemy group size (9, 10).

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In the conehead termite, *Nasutitermes corniger* (Motschusky 1855), the advantage of numerical superiority was somewhat less than predicted by the Square Law but greater than predicted by the Linear Law (estimated $\theta = 1.7$) (11). In this case, the mechanism of group size advantage also differed to that suggested by Lanchester, as individual killing power was increased by the presence of allies (11).

One important prediction arising from Franks and Partridge's (2, 3) modification of Lanchester's laws is the idea that the balance between group size and individual strength could be influenced by the environment. According to this prediction, complexity in the battlefield environment, such as tunnels, narrow corridors, or other tight spaces, should make it more difficult for larger armies to concentrate their attacks and outnumber their opponents in every engagement and should therefore push the balance in favor of individual strength (2, 3, 5). This effect of environmental complexity can be invoked to explain the "force-multiplying" effect of fortifications and fighting in urban environments in human conflict and is central to the strategy of smaller forces in "asymmetric warfare" where one army is heavily outnumbered and outmatched in a conflict (12–16). The importance of complex environments in potential conflicts even informs the design and development of urban areas in some cases (14).

In nonhuman animals, environmental complexity informs the evolution of different worker castes in social insects such that a single species can produce large numbers of small resource-cheap "minor" workers for conflict in the open, and smaller numbers of large and powerful "major" workers for conflict in confined spaces (17). In several species, such minor and major workers are differentially recruited to different combat situations, consistent with the predictions of Franks and Partridge (2, 3, 17–20). In an extreme case, members of the genus *Cephalotes* (also known as "turtle ants") have evolved a highly specialized defensive worker caste with a shield-shaped head to block and defend small nest entrances (21, 22). In a field experiment, relatively small ants with presumably low individual combat strength monopolized petri dish baits with large openings, while larger ants were more abundant at dishes with smaller openings that may have simulated fighting in constrained areas (23). While these results are consistent with the predictions of Franks and Partridge (2, 3), they do not constitute a controlled experimental test. Combat and fatalities of opposing forces were not measured, and therefore, the effect of environment on θ (Eq. **1**) could not be examined, and there could be no control of army size, species abundance, distance to sources of recruitment, or interference by nontarget species. Direct tests of the factors affecting group battles remain rare, even in social insects (5), and controlled experimental tests of the effect of environmental complexity on group battles are absent. As well as representing an important step in the field of nonhuman warfare research, such experiments may be relevant to the dynamics of non-native and native ants due to the following broadly recognized patterns. First, the human-mediated movement of ant species outside of their native ranges means that species with no evolutionary history of contact may be brought into conflict with each other, and the laws of group warfare have become relevant in these invaded areas. Second, non-native invasive ant species and populations are typically smaller and presumably individually weaker than native ants but tend to form extremely large colonies (5, 23–25). And third, human-induced habitat disturbance and simplification is associated with an increase in the relative abundance of non-native ants (26–29). Here, we provide a controlled empirical validation of the theoretical prediction that environmental complexity influences the trade-off between individual strength and group size, first in a computer-driven algorithm and then using a real-world ant model system.

Results

To illustrate the potential effects of environmental complexity on group combat in an idealized setting, we first arranged simulated battles using the real-time strategy video game Age of Empires II (30). In a series of 10 one-on-one duels between Elite Teutonic Knights (Knights; the infantry unit with the highest individual combat strength) and Two-Handed Swordsmen (Swordsmen; a mid-tier infantry unit with lower individual combat strength), all battles were won by Knights. Likewise, single Knights won all battles when opposed against one to four Swordsmen but lost all battles when opposed against five to 10 Swordsmen. From these data, the ratio of Swordsmen to Knights fighting strength was estimated as $\alpha_{THS}/\alpha_{TK} = 0.22$ (*SI Appendix*, Fig. S1).

For small groups of nine Knights, the probability of a Knights' victory decreased as the number of Swordsmen increased from 20 to 90 ($\chi^2_1 = 192.19$, $P < 0.001$; Fig. 1*A*), but the threshold number of Swordsmen at which Knights started to lose was higher in Complex than in Simple Arenas ($\chi^2_1 = 47.69$, $P < 0.001$; McFadden's (31) $R^2 = 0.84$; Fig. 1*A* and *SI Appendix*, Fig. S2). Proportion of Knight fatalities at the end of each battle increased from zero to one as the number of Swordsmen increased, but this increase was slower in Complex than Simple Arenas ($\chi^2_1 = 30.82$, $P < 0.001$; McFadden's (31) $R^2 = 0.81$; Fig. 1*B*). Likewise, fatalities of Swordsmen decreased as the number of Swordsmen increased, but this decrease was faster in Simple than in Complex Arenas ($\chi^2_1 = 61.34$, $P < 0.001$; McFadden's (31) $R^2 = 0.73$; Fig. 1*C*). We used nonlinear least squares (NLS) estimation to find the value of θ (Eq. **1**) based on our data in Simple and Complex Arenas. To test whether θ differed significantly between Simple and Complex Arenas, we used an *F* test to compare an NLS model in which θ was allowed to vary versus one in which θ was fixed. We found

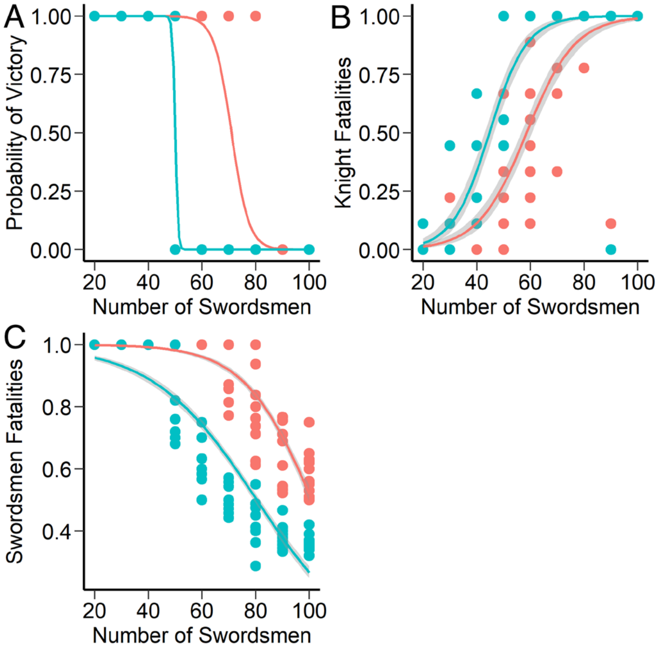

Fig. 1. Simulated group battles in simple (blue) and complex (red) arenas. (*A*) Probability of nine Teutonic Knights being victorious against increasing numbers of Two-Handed Swordsmen. (*B*) Proportion fatalities of Knights against increasing numbers of Swordsmen. (*C*) Proportion fatalities of Swordsmen as the number of Swordsmen increases. Computer simulations were carried out in the real-time strategy video game Age of Empires II (30).

that θ was significantly lower in Complex than in Simple Arenas (θ_{Simple} = 1.05 ± 0.03, $\theta_{Complex}$ = 0.87 ± 0.04, $F_{1,178}$ = 13.97, $P < 0.001$). Together, these results provide an idealized illustration of the prediction that investing in smaller armies of stronger soldiers is more effective in complex environments.

These trials, while not a test of how Lanchester's laws apply in the natural environment, are intended as a validation of Frank and Partridge's (2, 3) modifications of Lanchester's laws in a controlled simulation, in which the only relevant behavior displayed by soldiers is a "detect, move toward, attack" process. See *Materials and Methods* and *SI Appendix, Supplementary Methods* for a more detailed description of this simulated behavior. The results from this simple, idealized setting serve as a comparison to how these predictions might hold in the more complicated real-world system of ant battles.

We staged controlled battles between two co-occurring ant species: the Australian native meat ant, *Iridomyrmex purpureus* (Smith, F., 1858), and the non-native invasive Argentine ant, *Linepithema humile* (Mayr, 1868). *Iridomyrmex purpureus* is a dominant member of the Australian ant fauna in bushland habitats and undisturbed areas, and *L. humile* is a globally invasive pest species that displaces native ants in human-altered habitats. *Iridomyrmex purpureus* is a relatively large species (workers approximately 8 mm long) with a presumably high individual combat strength. *Linepithema humile* is many times smaller (workers approximately 2 mm long) but possesses an extraordinary "supercolony" social structure that virtually eliminates intraspecific competition and allows the recruitment of vast numbers of workers to competitive interactions (6, 32–39). Both *L. humile* and *I. purpureus* also possess a monomorphic worker caste, and the term "soldiers" is therefore used in this study to refer to individuals within armies, not to the specialized major workers of certain ant species (37). Selecting these two species as a model system for our experiments therefore ensured a clear difference in individual strength as a result of the large difference in body size (see below), as well as difference in group size.

We first performed a direct interspecific comparison of individual combat strength in ants. Previous studies have assumed that worker size correlates with combat strength (4, 5). *Iridomyrmex purpureus* workers were victorious in all one-on-one contests, except for five in which no combat was initiated. Combat was only ever initiated by *L. humile* workers. *Iridomyrmex purpureus* workers therefore have higher individual combat strength than *L. humile* workers. We could not estimate the ratio of *L. humile* to *I. purpureus* individual fighting strength as we did for the Age of Empires II (30) units since groups of *L. humile* seemed unwilling to engage with single *I. purpureus* in this setting, instead congregating at the lid of their containers (*SI Appendix, Supplementary Methods*). The reason for this lack of combat is unclear, as in all other experimental settings in this study the ants readily engaged with each other. As we were therefore unable to estimate a single value for α_{Lh}/α_{Ip}, we instead simulated a range of values for the purposes of estimating θ (see below).

When groups of 20 *I. purpureus* workers were opposed to groups of 5, 10, 20, 60, 100, 150, or 200 *L. humile* workers in Simple and Complex Arenas, all *L. humile workers* were dead after 24 h, but the number of fatalities of *I. purpureus* workers varied. Fatalities of *I. purpureus* increased as the number of *L. humile* increased (χ^2_1 = 5.08, P = 0.03; Fig. 2*A*), but fatalities were always lower in Complex than in Simple Arenas, even at low numbers of Argentine ants (χ^2_1 = 5.08, P = 0.02; Marginal R^2 = 0.08; Conditional R^2 = 0.28; Fig. 2*A*). We hypothesized that the effect of arena complexity even at low numbers of *L. humile* could be due to *L. humile* remaining clustered at small group sizes (*Discussion*). Filming and analyzing snapshots from an additional set of trials provided tentative support for this hypothesis. Clustering in small groups of 20 *L. humile* was not affected by the presence or absence of *I. purpureus* (χ^2_1 = 0.22, P = 0.66; *SI Appendix*, Fig. S3), but in all cases, *L. humile* were more clustered than predicted by a theoretical Poisson point distribution assuming complete spatial randomness (χ^2_1 = 17824.39, $P < 0.001$; *SI Appendix, Supplementary Methods* and Fig. S3). Whether the slope of the relationship between group size and group combat ability is affected by arena type can also be investigated by comparing estimates of θ (Eq. **1**). Using a stepwise process described in the *Materials and Methods* and *SI Appendix, Supplementary Methods*, we analyzed estimates of θ in terms of arena complexity and simulated α_{Lh}/α_{Ip} values, using a Gaussian linear model (LM). Mean and SE were calculated for predicted values and model coefficients from 10,000 iterations of this LM, with each iteration based on a new random sampling from uniform distributions of θ. This procedure is not amenable to a formal significance test per se, but the fact that the 95% CI around the mean coefficient of the linear α_{Lh}/α_{Ip} by Arena Complexity interaction did not overlap with zero was taken to indicate a significant

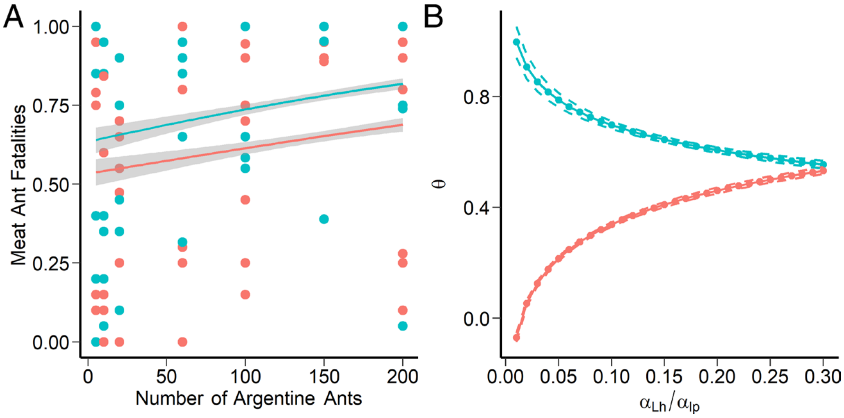

Fig. 2. Group battles between ants in simple (blue) and complex (red) arenas. (*A*) Proportion fatalities of workers in groups of 20 meat ant workers engaged in battles against increasing numbers of Argentine ant workers. (*B*) Estimates of Lanchester's θ. Points indicate estimates of θ (which describes the relationship between group fighting success and group size), based on a range of simulated values of the relative fighting strength of Argentine ant to meat ant workers (α_{Lh}/α_{Ip}). Fitted lines were calculated based on 10,000 iterations of random sampling from a uniform distribution around mean θ estimates. Dashed lines indicate SD of the iterated estimates.

Table 1. Mean coefficients and 95% CI from iterated NLS estimation of Lanchester's θ in terms of α_{Lh}/α_{Ip} and arena complexity in ant group battles

Term	Mean coefficient	Lower 95% CI	Upper 95% CI
Intercept	0.75	0.70	0.79
$\log(\alpha_{Lh}/\alpha_{Ip})$	0.18	0.16	0.19
Arena complexity	−0.35	−0.43	−0.27
Arena complexity × $\log(\alpha_{Lh}/\alpha_{Ip})$	−0.31	−0.35	−0.27

Estimates are based on 10,000 iterations of the model

interaction (Table 1). Plotting the predicted lines revealed that θ was lower in Complex than in Simple Arenas, and this difference was greater at lower values of α_{Lh}/α_{Ip}, when the simulated difference in individual combat strength of *I. purpureus* and *L. humile* was more pronounced (Fig. 2*B*). At very low values of α_{Lh}/α_{Ip}, $\theta_{Complex}$ was at its lowest and θ_{Simple} was at its highest. As α_{Lh}/α_{Ip} increased, θ_{Simple} declined and $\theta_{Complex}$ increased such that the curves converged (Fig. 2*B*).

Discussion

These results represent a fundamental advance in the empirical study of nonhuman warfare by providing controlled experimental evidence for an effect of environmental complexity on the outcome of group battles. Since *I. purpureus* workers have a higher individual combat strength than *L. humile*, our results are consistent with predictions that the environment can push the competitive balance in favor of different strategies, with complex, space-restricted battlefields favoring investment in stronger soldiers (2–5). It should be noted that this study was a two-species comparison, and future work would be enhanced by the inclusion of multiple species with varying levels of individual combat strength. Nevertheless, our results provide strong empirical evidence for an effect of environment on the application of Lanchester's laws to nonhuman warfare.

The results of the ant group battles are broadly consistent with the results of our simulated battles. One important difference between our simulated battle results and our ant results is that in the former, the effect of environmental complexity took the form of an arena-type by number of enemies interaction, whereas in the latter, the interaction was nonsignificant, and fatalities were lower in Complex Arenas across all numbers of enemies. In the ant battles, Complex Arenas seemed to favor the stronger *I. purpureus* workers even at low numbers of *L. humile* (Fig. 2*A*). Conversely, in simulated battles, Knight fatalities in Complex and Simple Arenas converged to zero at low numbers of Swordsmen, and the advantage of arena type was only seen as the number of Swordsmen increased (Fig. 1*B*). On the other hand, our analysis of θ in the ant battles suggests that particularly if *I. purpureus* workers are much stronger than *L. humile* workers (as suggested by the fourfold difference in body length and the fact that *I. purpureus* workers won 100% of one-on-one duels), environmental complexity does influence the slope of the relationship between group size and group combat ability. Furthermore, according to this analysis, the slope of θ against α_{Lh}/α_{Ip} was reversed across simple and complex environments. In complex environments, group size was relatively less important when the difference in individual strength was greater, as a more extreme increase in the size of the individually weaker army would be required to compensate for the greater strength of the opposing soldiers. It is unclear why the nature of this relationship should be reversed in simple environments such that the effect of a change in group size was relatively less when the difference in individual strength was greater. Nevertheless, our analysis of θ confirms our conclusion that group size is significantly more important in simple than in complex environments. Our estimates of θ were also lower than expectations based on Lanchester's laws and previous studies in ants (1, 3–5, 23), probably due to residual fatalities from sources other than combat (*SI Appendix, Supplementary Methods* and Fig. S6).

The patterns seen in the Age of Empires II (30) battles more closely match our expectation if fatalities are due only to the factors included in Lanchester's models, namely individual strength and group size (1). This is presumably because the behavior of soldiers in the simulated battles is extremely simple, with relevant behaviors limited by directions to move toward and attack any enemy within a detection radius, with no additional tactics or assessments at play. This section of the study is therefore intended as a demonstration of how Frank and Partridge's (2, 3) predictions, based on Lanchester's laws, would work in a simple, idealized setting with no complicating factors. Comparing these results to those of our ant battles, we can conclude that in the latter there may be additional factors involved that prevent us from achieving the same simplicity of results. For example, it is possible that even at very small numbers, *L. humile* workers stay clustered together and fight as a group, a tactic that would be more effective in Simple Arenas. This hypothesis is partially supported by the fact that in our additional filmed trials, *L. humile* were more clustered than predicted under a random Poisson point distribution. This tendency of *L. humile* to remain clustered even at small numbers may therefore help to explain the effect of Arena Complexity in our main experiment even when *I. purpureus* were not outnumbered. However, in the same filmed trials, the presence of *I. purpureus* did not induce increased clustering among *L. humile* compared to when *I. purpureus* were absent. Clustering therefore does not seem to be a result of combat tactics but rather a group behavior that persists regardless of the presence of enemies. The idea that additional factors, such as tactics, are present in the ant battles but not in the simulated battles would also explain the dramatic difference in R^2 between these two experiments. More complex analyses of battle tactics in empirical tests of group combat will be important for future studies. Filming experimental battles could be one way of achieving such an analysis, as demonstrated by Clifton et al. (11), who used video analysis to reveal that the killing power of individual *N. corniger* termites was increased by the presence of nestmates.

Unlike Knights, *I. purpureus* were never defeated in group battles. Across both our complex and simple environments, therefore, the smaller armies of stronger soldiers were more successful than the large armies of weaker soldiers, but the former suffered fewer fatalities in the complex environment. The conclusion that larger armies of weaker soldiers were more effective in the simple environment therefore refers to their success relative to how the same army type performed in the complex environment, as these large armies were seemingly never more effective than small armies of strong soldiers. The numerical battle types we were able to achieve were logistically constrained for our ant battles, and we were not able to introduce sufficiently high numbers of *L. humile* to defeat a group of 20 *I. purpureus*. This may seem surprising given that in the most extreme cases *L. humile* outnumbered *I. purpureus* by as much as 10 to one. As described above, however, *I. purpureus* workers are approximately four times the length of *L. humile* workers (*SI Appendix*, Fig. S4). According to the general length to weight scaling relationship for insects, this could translate to an almost 38-fold difference in body mass (40). Previous studies on ant combat have assumed that differences in size are correlated with differences in individual strength (4, 5). Here, we were able to validate this assumption by demonstrating that *I. purpureus* workers always won in one-on-one battles. As our study is a two-species comparison, however, generalizations are difficult because species-specific behaviors may also be important. For our group battle experiment, the difference in individual size and strength was apparently more important across environments than group size. This is contrary to the predictions of Lanchester's Square Law and to previous experimental work on termites (1, 11). Extending the experimental treatments to achieve *L. humile* victories could be informative for future work, and such an outcome could potentially be achieved by decreasing the number of stronger soldiers instead of (or as well as) increasing the number of weaker soldiers. Although *I. purpureus* were victorious in all group battles, the difference in *I. purpureus* fatalities across enemy group sizes and between complexity treatments still represents an important difference in the group fitness outcome of battles since an increase in fatalities represents a substantially higher cost of victory.

Our results may be of practical value in understanding the competitive balance between native and non-native species. *Linepithema humile* is one of the world's most important invasive ants, with global reported economic costs of more than US$19 million per annum (41). In Australia, the strongest native competitors of *L. humile* are typically other members of the dolichoderine group including *Iridomyrmex* species such as *I. purpureus* since they share similar ecological niches and resource requirements (6, 37, 42, 43). While *L. humile* is often more common in closer proximity to human habitations and *I. purpureus* is more common in rural and less disturbed areas, their distributions frequently overlap across Australia and direct conflict between our two target species is therefore common in nature (37, 42–46). *L. humile* is not confined to completely urbanized or degraded areas and can be found across a continuum of human-altered habitats in Australia and elsewhere across its non-native range (37, 42–46). In our study, for example, both species were sourced from the same field location (*SI Appendix*, *Supplementary Methods*). Furthermore, while both these species maintain large colonies, the "hypercooperative" social structure of *L. humile* means that its effective colony size is far superior, and it outnumbers its competitors in the vast majority of interactions (25, 35, 36, 47–49). The results of our study are therefore likely to be of direct relevance to interactions between our target species in nature.

More broadly, non-native invasive ant species are typically smaller than native species, and non-native populations of at least one species (*Wasmannia auropunctata*) are significantly smaller than native populations of the same species (24). If body size is correlated with individual combat strength in ants, non-native invasive ants would tend to have relatively low individual combat strength (2, 3, 5, 23, 24). The success of non-native invasive ants such as *L. humile* is attributed to their extremely large colonies and modified social structure that allows high recruitment, rather than competitive superiority of individual ants (23–25). According to Franks and Partridge's modifications of Lanchester's laws, therefore, non-native invasive ants should be particularly dominant in open battlefields, whereas native species may perform better in complex battlefields (2, 3, 5). This prediction is consistent with the results of our study and with evidence that human-induced habitat disturbance and homogenization is associated with an increase in the relative abundance of non-native ants (26–29). This pattern is expected to be at least partly due to release from competition from native species in previously disturbed areas (27), but if an effect of battlefield complexity also contributes, it may provide the potential for environmental manipulations to be integrated into invasive ant management programmes (23). For example, increasing habitat complexity in areas of incursion by invasive ants by adding natural or artificially constructed debris, revegetating areas with undergrowth, or contouring the ground surface into small alleyways or ridges could help tip the balance of aggressive interactions in favor of large native competitors. Alternatively, the prediction that smaller non-native ants may be more dominant in simplified or disturbed habitats could inform priority areas for management interventions. Advances in the management of non-native invasive ants are of global biosecurity significance since they constitute some of the most important pest animals in the world, with environmental, agricultural, economic, and health impacts equivalent to billions of dollars per year (44, 50–55).

Using ants, we have provided a controlled experimental test of an environmental effect on the outcome of group combat. Our results match expectations based on Franks and Partridge's modifications to Lanchester's laws (2, 3) that investing in stronger soldiers is more effective in complex than in simple battlefields. This was found to be the case in both our real-world ant model system and in our simulated battles. Our results could provide the basis for an expanding body of empirical research on the mechanics of group combat and the importance of the environment in deciding the outcome of battles. Future work could, for example, integrate the effect of battle tactics into the predictions of Lanchester's laws. Moreover, applying the results of our ant battles to a broader context of ant community dynamics where native and non-native species are present could provide alternative pathways for behaviorally integrated management of pest ants.

Materials and Methods

All raw data for this study are available as *SI Appendix*, *Supplementary Material*.

Simulated Battles. Simulated battles were constructed using The Age of Empire II Custom Scenario Builder (30). For a full description of this feature and the way in which our simulated battles were designed, see *SI Appendix*, *Supplementary Methods*. The way in which the behavior of units is coded is also described in more detail in *SI Appendix*, *Supplementary Methods*. For our trials, the relevant sections of code are those that direct units to move toward and attack the nearest enemy unit once enemies fall within a detection radius (four game tiles for Two-Handed Swordsmen and three game tiles for Teutonic Knights). For our trials, units were placed in such a way that enemies would be detected once each trial was initiated. We first confirmed that Teutonic Knights had higher individual strength than Two-Handed Swordsmen by performing a series of 10 one-on-one duels, all of which were won by Knights. Next, we determined the ratio of Swordsman to Knight fighting strength (α_{THS}/α_{TK}) by opposing single Knights to increasing numbers of Swordsmen and determining the threshold value at which the probability of victory was equal to 0.5 ($\alpha_{THS}/\alpha_{TK} = 0.22$; *SI Appendix*, Fig. S1). Finally, we opposed small armies of nine Knights against armies of 20, 30, 40, 50, 60, 70, 80, 90, or 100 Swordsmen in Simple (featureless) or Complex (with the battlefield divided by a series of uncrossable barriers) Arenas, with each battle type replicated 10 times (*SI Appendix*, Fig. S2 and Table S1). At the end of each battle, we recorded the outcome (Knights or Swordsmen victory) and the number of fatalities for each army.

For a full description of statistical analyses, see *SI Appendix*, *Supplementary Methods*. All statistical analyses were performed in R ver. 4.2.2 (56, 57). The probability of a Knights victory was analyzed in terms of arena type (fixed factor) and the number of Swordsmen (fixed covariate) using a binary GLM, with the significance of fixed effects assessed using Wald chi-square. The arena type by number of Swordsmen interaction was nonsignificant and was removed before continuing with the analysis ($\chi^2_1 < 0.001$, $P > 0.99$). Fatalities of Knights and Swordsmen were analyzed in terms of arena type and the number of Swordsmen using binomial GLMs. Overdispersion was tested by comparing the residual deviance to the residual degrees of freedom and was not considered to be significant if this ratio was less than two (58). Neither the Knight fatalities model (ratio = 0.64) nor the Swordsmen fatalities model (ratio = 0.65) was overdispersed.

We estimated the parameter (θ) describing the relationship between the number of units and group fighting ability according to the generalized version of Lanchester's laws (1, 5, 8). We estimated the value of θ for subsets of our data for Simple and Complex Arenas (θ_{Simple} and $\theta_{Complex}$) using NLS parameter estimation. To test whether θ differed significantly between Simple and Complex Arenas, we used an F test to compare an NLS model in which θ was allowed to vary with one in which θ was fixed.

Ant Battles. For a full description of ant collection and maintenance, experimental design, and statistical analysis of ant battles, see *SI Appendix*, *Supplementary Methods*. Workers were collected from six wild colonies each of *I. purpureus* and *L. humile* and maintained in the laboratory for the duration of the experiments. To determine the relative individual combat values of *I. purpureus* and *L. humile* workers, we staged 38 one-on-one contests between individual wild-caught *I. purpureus* and *L. humile* workers in sealed 1.5 mL Eppendorf tubes and observed each contest until one worker was killed. Neither *I. purpureus* nor *L. humile* workers possess stings or other chemical weapons, and in all cases, fighting consisted of opposing workers biting at each other, often targeting weak points such as legs and joints (6, 37). *Iridomyrmex purpureus* won all these contests, except in cases where combat was never initiated (*Results*). We attempted to determine the ratio of *L. humile* individual strength to *I. purpureus* strength (α_{THS}/α_{TK}) using the same methods as described for the simulated battles, but groups of *L. humile* were unwilling to engage in combat with single *I. purpureus*. For the purposes of estimating θ_{Simple} and $\theta_{Complex}$ for our ant data, therefore, we simulated a realistic range of α_{THS}/α_{TK} values from 0.01 to 0.3, in increments of 0.01 (see below).

Next, we tested how environmental complexity and relative army size affected the outcome of battles between groups of *I. purpureus* and *L. humile.* Groups of 20 *I. purpureus* workers were opposed against groups of 5, 10, 20, 60, 100, 150, or 200 *L. humile* workers in 10 L plastic containers with either a flat ground surface (Simple Arenas; *SI Appendix*, Fig. S5*A*) or with strips of wooden board glued to the bottom of the container at 10 mm intervals to form artificial laneways (Complex Arenas; *SI Appendix*, Fig. S5*B*). While these boards were not impenetrable barriers for the ants, they served to make a realistically complex environment. Observations of the battles confirmed that combat took place almost exclusively in the laneways between obstacles, as intended. Between four and eight group battles were performed for each treatment combination (93 battles in total; *SI Appendix*, Table S2). Dead versus surviving ants were counted after 24 h (*SI Appendix*, Fig. S4), following Plowes and Adams (8). We analyzed *I. purpureus* fatalities in terms of arena type (fixed factor) and the number of *L. humile* (fixed covariate) using a binomial GLMM, with *I. purpureus* source colony and *L. humile* source colony included as random effects to account for the hierarchical structure of the design. The model was overdispersed (ratio = 7.114), and this was accounted for by including an individual level random effect. The significance of fixed effects was again assessed using Wald chi-square. The arena type by number of *L. humile* interaction was nonsignificant and was removed ($\chi^2_1 = 0.87$, $P = 0.97$). A simulated power analysis reported a power level of 0.88 (lower CI = 0.86, upper CI = 0.90; *SI Appendix*, *Supplementary Methods* and Fig. S7) for the interaction effect at our sample size, with simulated power of main effects greater than that for the interaction.

We estimated θ_{Simple} and $\theta_{Complex}$ for our ant data using a stepwise process, a full explanation of which is provided in *SI Appendix*, *Supplementary Methods*. Because groups of *L. humile* would not reliably engage with single *I. purpureus*, we were not able to obtain a single estimate of α_{Lh}/α_{Ip} for use in estimation of θ_{Simple} and $\theta_{Complex}$ (see above and *SI Appendix*, *Supplementary Methods*). We instead simulated α_{Lh}/α_{Ip} estimates in a realistic range from 0.01 to 0.3, in increments of 0.01. NLS estimation was used to calculate estimates of θ_{Simple} and $\theta_{Complex}$ (and SE) for each value of α_{Lh}/α_{Ip}. Uniform distributions were generated based on these estimates of θ_{Simple} and $\theta_{Complex}$, and one estimate of θ was randomly sampled from each distribution. Next, we used a Gaussian linear model to analyze these estimates of θ in terms of α_{Lh}/α_{Ip} and Arena Complexity and extracted the predicted values of θ, the intercept coefficient, and the slope coefficient for each term in the model. This process, from the formation of the uniform distributions to extraction of model terms, was repeated across 10,000 iterations. Next, we plotted fitted lines (with SD) of θ_{Simple} and $\theta_{Complex}$ against α_{Lh}/α_{Ip} (Fig. 2*B*). The significant effect of Arena Complexity on θ was inferred from the fact that the CI around the slope of the Arena Complexity by α_{Lh}/α_{Ip} (linear term) interaction did not overlap with zero (Table 1). We also filmed an additional set of experimental trials to investigate whether Argentine ants remained clustered during combat. Five six-hour trials were filmed in which 20 *L. humile* were opposed to 20 *I. purpureus* and five trials in which no *I. purpureus* were present. Clustering of *L. humile* at hourly intervals was compared between *I. purpureus* presence treatments and to a Poisson point distribution assuming complete spatial randomness. For a description of these additional trials, see *SI Appendix*, *Supplementary Methods* and Fig. S4.

Ethics Statement. This research conforms to the animal ethics requirements of the University of Western Australia and CSIRO. Under Western Australian law, the use of invertebrates (other than decapods and cephalopods) in research does not require animal ethics approval.

Data, Materials, and Software Availability. All study data are included in the article and/or supporting information. Data and R code are also publically available at in the Dryad Research Repository at https://doi.org/10.5061/dryad.fttdz08zx (59).

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